

Ontogeny of Diving and Feeding Behavior in Juvenile Seaturtles: Leatherback Seaturtles (*Dermochelys coriacea* L) and Green Seaturtles (*Chelonia mydas* L) in the Florida Current

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We compared activity, diving behavior and response to prey by *Dermochelys coriacea* and *Chelonia mydas* during their first 8–10 weeks of development. We reared juveniles in the laboratory and, at two-week intervals, released them in the ocean for a brief trial. Each turtle towed a device used to measure its dive profile. All turtles swam throughout their trials, but *D. coriacea* swam more slowly than *C. mydas*. *Dermochelys coriacea* dives had V-shaped profiles and older turtles made longer and deeper (up to 18 m) dives than younger turtles. *Chelonia mydas* dives were usually shallow (<6 m) and consisted of three (V, S, and U) profiles. Older *C. mydas* made dives that were longer but only slightly deeper than those of younger turtles. *Dermochelys coriacea* fed throughout the water column exclusively on gelatinous prey *Aurelia*, ctenophores, and unidentified gelatinous eggs. *Chelonia mydas* fed near the surface on floating *Thalassia* and *Sargassum* or at shallow depths on ctenophores and unidentified gelatinous eggs but ignored large jellyfish (*Aurelia*). Thus, early in development the two species overlap in foraging area and in diet. However as *D. coriacea* grow they dive deeper where prey assemblages probably differ from those in shallow water where *C. mydas* feed. These distinct behavioral trajectories probably cause the niches of *D. coriacea* and *C. mydas* to separate spatially very early in their development.

The beaches of southeastern Florida serve as rookeries for populations of Green Seaturtle (*Chelonia mydas* L.), Leatherback Seaturtle (*Dermochelys coriacea* V.) and Loggerhead Seaturtles (*Caretta caretta* L.; Meylan et al., 1995). After emerging from nests, their hatchlings crawl to the surf zone, then migrate offshore during a 24–36 h “swimming frenzy” (Wyneken and Salmon, 1992). Hatchlings eventually encounter the Florida Current (western portion of the Gulf Stream) that probably carries them to open water “nursery” habitats (Witham, 1980; Musick and Limpus, 1997). Except for *C. caretta*, the geographic location of marine turtle nursery habitat in the pelagic is unknown, as is how and where foraging occurs in the water column. Both sources of information are essential for defining the ecological niche of *D. coriacea* and *C. mydas* (Brown, 1995).

Juvenile *D. coriacea* (≤ 100 cm in curved carapace length [CCL]) have been seen at low latitudes (6–14°) in the open ocean where water temperatures are relatively high (26–36°C). As they grow sightings shift to higher latitudes where temperatures are variable and often cooler (Eckert, 1999). Swimming *D. coriacea* likely stay

in open water where there are no obstructions because in captivity they do not recognize and have difficulty escaping from physical barriers (Witham, 1977).

Posthatchling *C. mydas* are so rarely observed in the ocean that their nursery habitats are unknown. Some sightings have been near *Sargassum* driftlines (Caldwell, 1969; Carr, 1986b; Carr and Meylan, 1980) but the counter-shading of young *C. mydas* indicates they probably forage in open water (Musick and Limpus, 1997). In laboratory studies, *C. mydas* avoid contact with flotsom (Mellgren et al., 1994). Witherington (2002) found no posthatchling *C. mydas* where *C. caretta* of that age were abundant (drift lines in the Florida Current), suggesting the two species occupy different habitats.

To our knowledge, the behavior of posthatchling *D. coriacea* and *C. mydas* has not been observed in deep, open ocean habitats. We reared hatchlings of both species in the laboratory to gain insights into how the two species might differ in habitat use. At intervals of approximately two weeks, turtles were transported several kilometers offshore to the Florida Current to observe their diving and feeding behavior. Our goals were to determine (1) how the two species differed in their use of space while swimming, diving, and feeding, and (2) how their behavior changed as they increased in size and age.

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MATERIALS AND METHODS

Maintenance.—We reared 34 hatchlings (1–8 per nest from 11 nests) of *D. coriacea*, using previously described methods (Jones et al., 2000). Hatchlings were obtained from nests located in Palm Beach County, Florida, between July and August 1998 and 1999. We individually marked hatchlings on the carapace with distinct dot patterns of white correction fluid (“liquid paper”). Hatchlings were housed in groups of four with circular plastic pools (1.5 m wide \times 30 cm deep). Pools were filled with 103 liters of filtered and sterilized seawater, partially changed every three days. Water temperature was maintained between 23° and 27°C. Turtles were fed once daily to satiation using a gelatin-based artificial diet (Jones et al., 2000).

We captured 33 *C. mydas* (4–13 per nest) as they emerged between August and September from five nests in Palm Beach County. Turtles were placed in a large, circular (2.5 m wide \times 30 cm deep) plastic pool, continuously supplied with fresh, sand-filtered seawater. We marked each hatchling with a small (7.0 mm²) uniquely colored and numbered plastic strip fixed to its carapace with a drop of cyanoacrylic cement. We fed juveniles (defined as posthatchlings that had commenced feeding) raw shrimp once daily to satiation, and maintained the turtles on a 14:10 L:D photoperiod at 22–26°C.

Dermochelys coriacea used in trials were (age in weeks/number of turtles): 2/5, 4/12, 6/7, 8/6, and 10/4. At two weeks of age, juveniles were (mean \pm SD) 59.6 \pm 9.45 g in mass and 72.5 \pm 5.0 mm in SCL. At 10 weeks of age, the turtles more than doubled in mass and increased in SCL by \sim 30%. Growth curves for this species are presented elsewhere (Jones et al., 2000).

Chelonia mydas used in trials were 2/9, 4/8, 6/8, and 8/8. Turtles increased from 34.8 \pm 6.6 g in mass and 62 \pm 3.5 mm in SCL at two weeks of age to 70.2 \pm 24.4 g and 79.1 \pm 11.4 mm in SCL at eight weeks of age.

Field Trials.—Between late August and early November, we transported 2–4 juveniles from two or more nests to sites 4–6 km offshore and within the Florida Current (depth: 100–200 m). Turtles were not fed for 24 h prior to transport. Sites were adjacent to Boynton Beach, Palm Beach County, Florida (26°30'N lat., 80°00'W long.). On the boat the turtles were housed in a 182-liter live well, filled with continuously circulating seawater. Total transport time was \leq 1.5 h.

Releases took place during the midmorning or early afternoon. *Dermochelys coriacea* were given a 30-min trial. *Chelonia mydas* were given 35-min trials because they sometimes made a single long, deep dive immediately after release. Thereafter,

their dives were relatively shallow and short. Therefore, we gave them 5 min to acclimate to their oceanic surroundings. At the conclusion of their trial (or their last dive, if it was initiated just before the trial ended), juveniles were released (after removing plastic tags or white markings).

During trials, two observers wearing masks and snorkels followed 4–6 m behind the turtles. Both observers remained at the surface. One held a spool containing 70 m of 7-kg test line, which was attached to our depth-recording device towed by the turtle. Sufficient line was released while the turtle was diving (swam downward to a depth \geq 0.5 m) so that its descent was unimpeded. Line was retrieved when the turtle surfaced. The second observer used hand signals to indicate the beginning and end of each dive to a third observer, driving the boat about 10 m behind both swimmers. Water clarity was sufficient for swimmers to see diving juveniles during all but their deepest dives.

Dive Measurement.—We measured dive profiles using two devices. In 1998, 14 *D. coriacea* towed an air-filled aluminum cigar tube 150 mm long \times 15 mm in diameter. We glued a 1.0 m length of 2.3-kg test monofilament to the front of the tube and attached the other end to the turtle's carapace with a small VelcroTM patch. This line was designed to break if a predator took the turtle. The cigar tube was rendered neutrally buoyant by the addition of internal weights and balanced so that the tube floated horizontally in the water column. Dive profiles were measured by pointing a sonar unit (Furuno FE-4200, Hyogo, Japan) at the cigar tube during the dive. Records were stored on a chart recorder housed on the boat.

During the 1999 field season, 20 *D. coriacea* towed a miniature time-depth recording (TDR) tag (Lotek LTD 100, Newfoundland, Canada; 57 mm long \times 18 mm in diameter; mass under water, 1 g). The tag was attached to the turtle by a 1.0-m length of fine monofilament, ending in a velcro patch that adhered to its carapace (Fig. 1). In 2000, we used the tag to measure *C. mydas* dives. It was attached to the turtle by a 1.0-m length of fine monofilament line that encircled its body behind the foreflippers.

We made the tag neutrally buoyant for *D. coriacea* (whose consecutive dives were usually separated by several min at the surface) and slightly positively buoyant for *C. mydas*. Positive buoyancy enabled the tag to reach the ocean surface between consecutive *C. mydas* dives, which often were initiated after only a short (1–2 sec) pause to breathe.

The TDR recorded pressure and time at 10-sec (*D. coriacea*) or 2-sec (*C. mydas*) intervals. Records were downloaded and stored on a computer.

Behavioral observations were documented as field notes and by underwater photography.

Drag imposed by the tag, tether, and cigar tube probably decreased swimming speed and may have affected dive depth. We balanced these disadvantages against the following advantages. First, tethering eliminated the possibility that a turtle might escape during a trial by diving beyond our visual range. Second, a TDR was the least intrusive method for measuring dives. The alternative (following the turtle using SCUBA and completing measurements by instruments we carried) increased the possibility that the observer might affect the turtle's behavior. Third, our purpose was to determine how the two species differed in diving, swimming, and associated behavior, not to measure maximum swimming speed or dive depth.

Data Analyses.—Dive parameters (descent speed; duration; depth; profiles) were measured from the TDR or chart records. Descent speed (cm/sec) was based upon the actual (for turtles diving once) or average (for turtles diving more than once) time to descend to depth. Dive profiles were classified using the criteria of Hochscheid et al. (1999).

Statview© (Abacus Concepts, Berkeley, CA) was used to compute correlation coefficients for dive parameters (duration vs. depth). Mean dive depth, dive duration and descent speed was calculated for each turtle. An ANCOVA was then used to determine whether the two species differed in these attributes as a function of age, with mass as the covariate. Mann-Whitney, Kruskal-Wallis, and Chi-square tests (corrected for continuity; Siegel and Castellan, 1988) were used to specify more precisely how dives changed with age.

RESULTS

Swimming Behavior.—Juveniles of both species swam and made dives by "powerstroking" (synchronous movements of the foreflippers; Wyneken, 1997). During trials, *D. coriacea* swam slowly near the surface with little change in direction. Diving was accomplished with no obvious change in stroke rate or swimming speed. *Chelonia mydas* also swam near the surface but more rapidly, often changing speed and direction. Diving was initiated by a brief but abrupt increase in stroke rate and speed, followed by continued descent to depth at a slower speed.

Diving Frequency.—Twenty-one of 34 *D. coriacea* (62%) made dives (mean \pm SD for the diving turtles = 4.10 ± 2.53 dives/trial, range = 1–9; $N = 86$ dives). Diving frequency did not change with age (nine of 17 turtles < 4 weeks vs. 12 of 17 turtles > 4 weeks of age; n.s. by a χ^2 -test). All

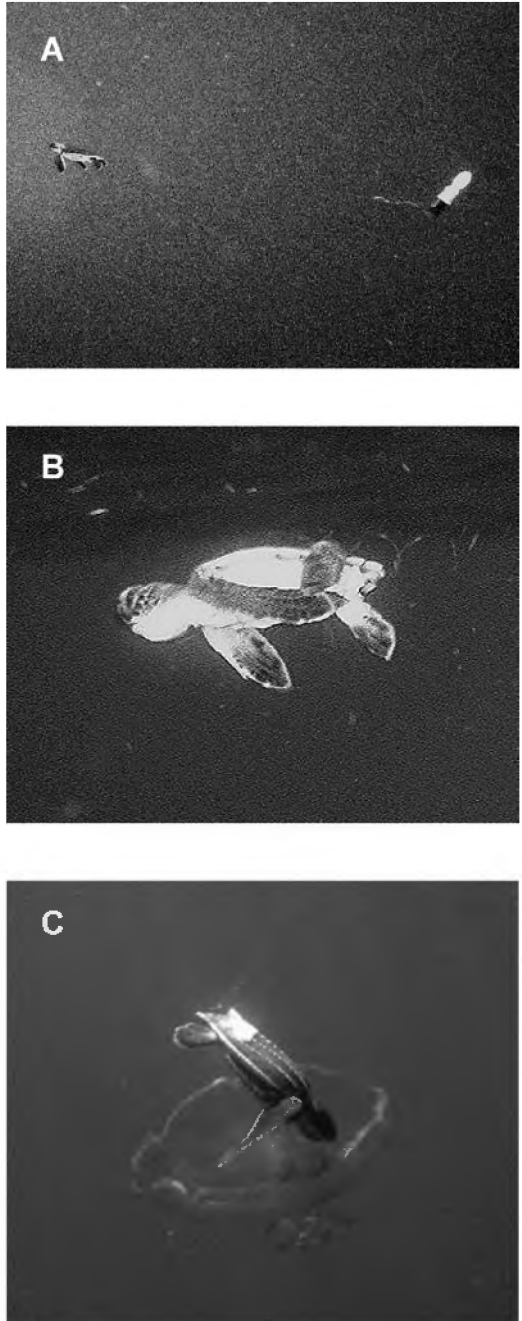


FIG. 1. Green turtles (A, B) and a leatherback (C) in the Florida Current. (A) Turtle towing a TDR. Camera angle makes the tag appears large relative to the turtle. (B) *Chelonia mydas* feeding on gelatinous eggs near the surface (note expanded gular region). (C) *Dermochelys coriacea* feeding on *Aurelia*.

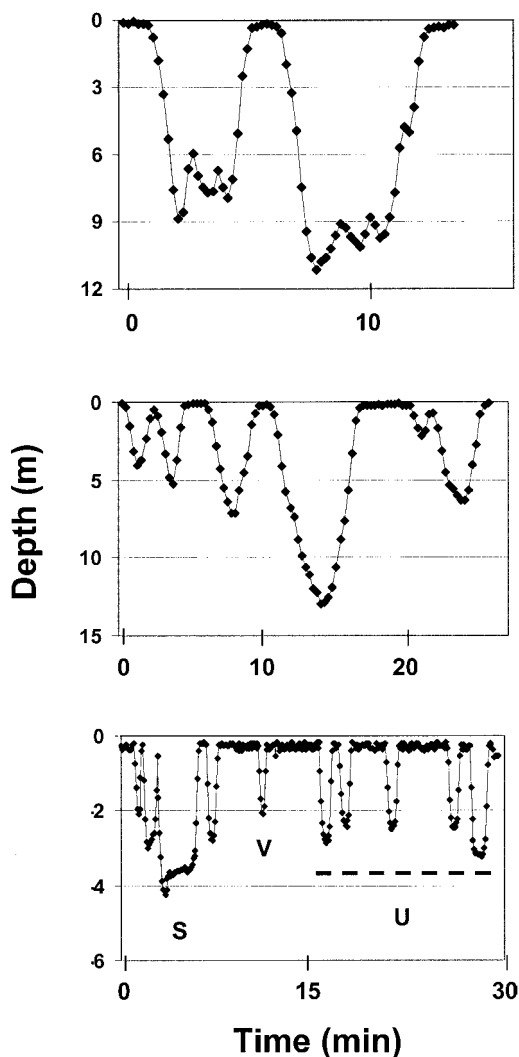


FIG. 2. Dive profiles. Top and middle, W- and V-dives of two *Dermochelys coriacea*. Bottom: S-, V-, and U-dives of a green turtle. Consecutive readings (filled diamonds) are at 10-sec (*Dermochelys coriacea*) and 2-sec (*Chelonia mydas*) intervals.

green turtles made dives during their trials (9.1 ± 5.46 ; range = 1–25; $N = 299$). Diving frequency did not change with age (148 dives by 17 turtles < 4 weeks vs. 151 dives by 16 turtles > 4 weeks; n.s. by a χ^2 -test).

The two species differed significantly in the number of dives made by diving turtles (86 dives by 21 *D. coriacea*; 299 dives by 33 *C. mydas*; $\chi^2 = 15.14$, $P < 0.001$, 1 df).

Dive Profiles.—Profiles were obtained for 71 of 86 *D. coriacea* dives. Most ($N = 62$, or 87 %) were V-dives (Fig. 2); the remainder were W-dives that included small changes in vertical position once

turtles reached depth. In five W-dives, the turtles were feeding at depth on jellyfish.

Chelonia mydas showed three dive profiles: V ($N = 141$), U ($N = 119$), and S ($N = 20$; Fig. 2). Nineteen others could not be classified. S-dives were 2.5–5.5 m in depth, and 20–200 sec in duration while V- and U-dives were 0.5–9.3 m in depth and 15–260 sec in duration. However, over 90% of these dives were shallower (≤ 5.0 m) and shorter (≤ 180 sec). V-dives were significantly shallower (Mann-Whitney $Z = -4.35$, $P < 0.001$) and shorter ($Z = -7.52$, $P < 0.001$) than U-dives. Two *C. mydas* made especially deep V-dives during the acclimation period and two after their trial ended (to evade recapture). These were the longest (561 sec by an eight-week-old turtle) and deepest (18.7 m by a four-week-old turtle) dives we observed in this species.

Comparisons in Descent Speed, Duration, and Dive Depth.—The two species differed significantly in descent speed (Table 1). Average descent speed (mean \pm SD) for 21 *D. coriacea* was 7.08 ± 3.20 cm/sec (range: 3.4–16.2 cm/sec). For 32 *C. mydas*, it was 21.26 ± 9.66 cm/sec (range: 8.2–40.8 cm/sec).

Dive duration was positively and significantly correlated with dive depth in both *D. coriacea* ($N = 86$, $r = 0.82$, $P < 0.01$) and *C. mydas* ($N = 299$, $r = 0.69$, $P < 0.01$; Fig. 3). Most dives by both species were shallow (≤ 6 m) but in *D. coriacea* many were deeper (up to 17.1 m). *Chelonia mydas* did not dive deeper than 9.3 m (Fig. 3).

Dive duration (Table 2) and dive depth (Table 3) differed significantly between the species. In *D. coriacea*, dives were on average deeper (5.29 ± 3.37 m) and longer (128.14 ± 84.38 sec) than those of *C. mydas* (2.47 ± 1.16 m, 82.21 ± 27.60 sec).

Diving as a Function of Age.—Descent speed (Table 1), dive duration (Table 2), and dive depth did not differ significantly with age (Table 3). However, these analyses were based upon means of each behavior for individual turtles. The raw data (Fig. 3) suggested that at least for *D. coriacea*, older turtles most often made the deepest and longest dives. Because in both species most dives were relatively short (≤ 200 sec) and shallow (≤ 6 m), mean values may have masked these contrasts.

The data were reexamined by comparing the distribution of the deepest and longest dive made by each turtle, as a function of its age. In *D. coriacea*, the deepest dive made by each younger (2–6 weeks) turtle ranged between 1.2 and 15.2 m ($N = 13$ turtles, mean = 5.75 m), whereas the deepest dive made by each older (7–10 weeks) turtle ranged between 6.3 and 17.1 m ($N = 8$, mean = 10.65 m). Older turtles made significantly deeper dives (Wilcoxon $Z = -2.68$, $P = 0.003$). The longest dive made by each younger *D. coriacea* ranged from 15–360 sec ($N = 13$,

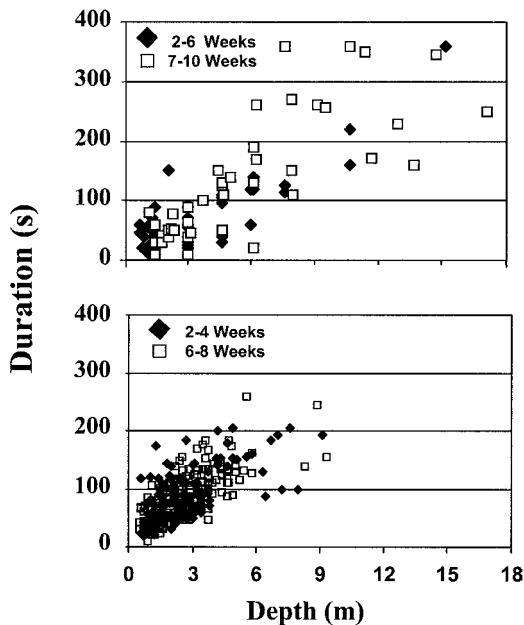


FIG. 3. Dive depth and duration shown by *Dermochelys coriacea* (above, $N = 45$ dives by younger and 41 dives by older turtles) and by *Chelonia mydas* (lower, $N = 148$ dives by younger and 151 dives by older turtles).

mean = 119.23 sec) whereas among older turtles the range was 170–360 sec ($N = 8$, mean = 256.5 sec). Older turtles made longer dives (Wilcoxon $Z = -3.15$, $P = 0.001$).

In *C. mydas*, the same trends were apparent although absolute differences between the age groups were less extreme. The deepest dive made by each younger (2–4 weeks) turtle ranged between 1.3 and 9.1 m ($N = 17$ turtles, mean = 5.07 m), whereas among older (6–8 weeks) turtles, it ranged between 1.1 and 9.3 m ($N = 16$, mean = 5.54 m). Older turtles made significantly deeper dives (Wilcoxon $Z = -1.80$, $P = 0.04$). The longest dive made by each younger *C. mydas* ranged from 40–204 sec ($N = 17$, mean = 102 sec), whereas among older turtles, the range was 68–258 sec ($N = 16$, mean = 149.6 sec). Older turtles made significantly longer dives (Wilcoxon $Z = -2.72$, $P = 0.003$).

Although V-dives were the dominant profile among *D. coriacea* regardless of age, dive profiles changed with age in *C. mydas*. Younger (2–4 weeks; 148 dives observed) juveniles made more V- ($N = 99$) than U- ($N = 40$) dives, whereas older (6–8 weeks; 151 dives observed) juveniles made fewer V- ($N = 42$) than U- ($N = 79$) dives ($\chi^2 = 33.3$, $P < 0.001$, 1 df).

Feeding Behavior.—Nine *D. coriacea* fed during trials. Two ate ctenophores (*Ocyropsis* or *Mne-*

TABLE 1. ANCOVA summary table for determining the effects of species, age, and their interactions on diving descent speed of *Chelonia mydas* and *Dermochelys coriacea*, 2–8 weeks of age.

Source of variation	MS	df	F	P
Covariate (mass)	218.50	1	3.74	0.061
Species	1433.98	1	20.70	0.0001
Age	178.39	3	1.25	0.307
Species \times age	39.53	3	0.1	0.189

TABLE 2. ANCOVA summary table for determining the effects of species, age, and their interaction on dive duration of *Dermochelys coriacea* and *Chelonia mydas*, 2–8 weeks of age.

Source of variation	MS	df	F	P
Covariate (mass)	9334	1	2.31	0.136
Species	29077	1	7.96	0.007
Age	28479	3	2.52	0.072
Species \times age	14678	3	1.67	0.189

TABLE 3. ANCOVA summary table for determining the effects of species, age, and their interaction on dive depth of *Dermochelys coriacea* and *Chelonia mydas*, 2–8 weeks of age.

Source of variation	MS	df	F	P
Covariate (mass)	15.888	1	1.32	0.258
Species	54.069	1	14.92	0.0001
Age	29.474	3	1.33	0.278
Species \times age	22.604	3	1.43	0.248

niopsis) and one ate gelatinous (probably molluscan) eggs. Six turtles fed on moon jellyfish (*Aurelia*; Fig. 1). Feeding was observed at depths between 0.5 and 14 m.

Seven *C. mydas* fed during their trials, all ≤ 2 m below the ocean surface (Fig. 1). Two turtles nibbled on floating *Sargassum* and *Thalassia* leaves suspended just below the surface. One turtle consumed a ctenophore and four others fed on gelatinous eggs. *Chelonia mydas* ignored *Aurelia*, even when jellyfish were abundant.

DISCUSSION

Constraints.—All juveniles were reared in shallow tanks and had no opportunity to dive before they were released in the ocean, which might have modified their performance. In addition, differences in how long turtles were held in captivity might affect their performance at different ages. However, all turtles swam normally, most made dives, and some consumed natural prey. We saw no behavior that appeared “abnormal.” Differences between species in

behavior seemed appropriate given our current understanding of their ecological specializations. These results suggest that although turtles were reared under artificial conditions, unique features of their behavior persisted.

Activity.—Previous studies on *D. coriacea* and *C. mydas* have revealed correlations between activity level and locomotion on the one hand and O_2 consumption on the other. Wyneken (1997) classified *D. coriacea* as “marathon” and *C. mydas* as “sprinter” strategists with regard to their locomotion and energetics. During their frenzy period, *D. coriacea* hatchlings swim at relatively slow (~ 25 cm/sec), but constant speeds, consume little oxygen, and show small changes in O_2 consumption between rest and activity (“narrow” aerobic scope; Wyneken and Salmon, 1992; Wyneken, 1997). *Chelonia mydas* during their frenzy period swim faster (~ 44 cm/sec), consume $2\times$ more oxygen than *D. coriacea* and show a larger change in O_2 consumption between rest and activity (“wide” aerobic scope). Postfrenzy *C. mydas* consumed more oxygen than postfrenzy *D. coriacea* (Wyneken, 1997).

Our observations were both qualitatively and quantitatively consistent with these assessments. Juveniles of both species swam throughout trials, but *D. coriacea* swimming and diving speeds were slower than those shown by *C. mydas*. Many *D. coriacea* did not dive during their trials, whereas all of the *C. mydas* did. Diving green turtles also averaged almost twice as many dives/trial than did diving *D. coriacea*. Most *D. coriacea* dives were short (< 100 sec in duration) and completed over a small portion of the trial. Few dives made by either species resulted in prey capture, although some prey consumed by both species were always present. Thus, differences in diving frequency between species probably were not caused by variation in prey abundance.

Dive Profiles.—V-dive profiles of juvenile *D. coriacea* were similar to those of adult *C. mydas* diving in deep water (Eckert et al., 1986, 1989). The few W-dives we witnessed have not been seen in adult turtles. In more than half (five of nine) of these dives, juveniles were feeding. We suggest that W-dives occur when juveniles either find food, or while they assess prey abundance at depth (as occurs in other diving vertebrates; Thompson and Fedak, 2001). V-dives were rarely associated with feeding, and so their function remains unclear.

Juvenile *C. mydas* performed V-dives that, in contrast to *D. coriacea*, were typically shallow and brief. They also showed S- and U- dives that were never observed in juvenile *D. coriacea*, but occur among internesting *C. mydas* (Hochscheid et al., 1999; Hays et al., 2000) in shallow water.

Dermochelys coriacea also make U-dives under the same conditions (Eckert, et al., 1996). Whether profiles of juvenile *C. mydas* are functionally similar to those of adults remains unknown. Juveniles showed U- and S-dives even in deep water, where there was no depth barrier.

Age, Depth, and Duration.—The shallow dives of juvenile turtles might reflect physiological constraints to deep diving. Alternatively, they might result from a behavioral preference for shallow dives that are well within physiological limits. Larger marine turtles make deeper (leatherbacks; Eckert et al., 1986) and longer (hawksbills; van Dam and Diez, 1997) dives than smaller conspecifics. In general, small body size should limit diving depth and duration because (1) the volume of tissue to store oxygen is lower, and (2) mass-specific metabolic rates of smaller animals are higher (Schmidt-Nielsen, 1997). Thus, we expected that larger and older *D. coriacea* and *C. mydas* would show longer and deeper dives than younger turtles; this prediction was fulfilled.

In both species, older turtles most often made the deepest and longest dives. This tendency, however, was more obvious among *D. coriacea* (whose dives exceeded 17 m) than among *C. mydas* (whose dives did not exceed 9 m; Fig. 3). Most *D. coriacea* dive profiles were V-shaped, and therefore longer dives were accompanied by a proportional increase in dive depth. In older *C. mydas*, however, most dives had U-shaped profiles so that longer dives were accompanied by only a modest increase in depth.

Although juvenile size must ultimately limit dive depth and duration in both species, the contrasts we witnessed are best explained by behavioral preferences. *Chelonia mydas*, when sufficiently motivated, were capable of dives that were comparable in depth and duration to the deepest dives made by leatherbacks. In the absence of that motivation (i.e., during “routine” diving), *C. mydas* chose to remain closer to the ocean surface.

Behavioral Ecology of Diving.—Our results suggest that, during their first weeks in the pelagic, *D. coriacea* diving capacities increase rapidly with growth. During this time, they feed opportunistically on prey located between the surface and the dive depths that they can achieve, which probably are within ~ 20 m of the surface. “Outgrowing” these constraints may select for faster growth rates in *D. coriacea* than in the hard-shelled marine turtles (Rhodin, 1985). We probably witnessed the onset of that process, one which ultimately leads to adult turtles feeding over a broad range of depths (near the surface [Eisenberg and Frazier, 1983; Limpus, 1984; Grant and Ferrell, 1993; Grant et al., 1996] and in the deep-scattering layer [Eckert et al.,

1986, 1989]) and latitudes (Bleakney, 1965; Pritchard, 1976; Brongersma, 1972; Hodge, 1979).

For *C. mydas*, the trend was clearly different. As turtles aged, dive duration increased faster than dive depth. Pelagic-stage *C. mydas* probably search for and forage upon prey found relatively close (≤ 5 m) to the ocean surface.

Thus, even at an early age *D. coriacea* and *C. mydas* differed in where they foraged and in the prey that they consumed. *Dermochelys coriacea* fed exclusively on gelatinous prey, whereas *C. mydas* foraged on floating or suspended algae, as well as smaller animal prey at or near the surface. Similar results have been reported elsewhere (Hughes, 1974; Frick, 1976), suggesting that young *C. mydas* are omnivores with a tendency toward carnivory, whereas young *D. coriacea* are gelatinivores (Bjorndal, 1997). Differences in prey category, prey size, and foraging depth appear to be primary niche axes separating these pelagic turtles.

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A New Species of *Tantilla* (Serpentes; Colubridae) of the *Taeniata* Group from Southern Belize

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ABSTRACT.—A new snake of the genus *Tantilla* is described from southern Belize. This species, a member of the *taeniata* group, is characterized by a dark gray-brown, almost black ground color; a narrow pale middorsal stripe confined to the vertebral scale row; a narrow pale lateral stripe on adjacent thirds of the third and fourth scale rows; a broad pale nape band that is complete medially; dark mottling on the lateral edges of the ventrals; and 153 ventrals + 64 subcaudals in the single known specimen, a female. It is most similar to *Tantilla impensa* of southern Chiapas, the central Guatemalan ranges and western Honduras but differs from this species in its darker overall color pattern, the presence of dark mottling on the lateral edges of the ventrals, and in having a lower number of ventrals.

RESUMEN.—Se describe una nueva especie del género *Tantilla* del sur de Belice. Esta especie pertenece al grupo *taeniata* y se caracteriza por lo siguiente: color oscuro gris-café, casi negro; una estrecha franja pálida mediodorsal confinada en la fila vertebral de escamas; una estrecha franja pálida lateral en los tercios adyacentes de las filas de escamas tercera y cuarta; una ancha banda pálida en la nuca, completa medialmente; moteaduras oscuras en los bordes laterales de los ventrales y 153 ventrales + 64 subcaudales en la única hembra conocida. Es similar a *Tantilla impensa* con una distribución en el sur de Chiapas y centro de Guatemala hasta el oeste de Honduras, de la que se diferencia por su color más oscuro, presencia de moteaduras oscuras en los bordes laterales de los ventrales y por tener un menor número de ventrales.

In terms of its overall composition, the herpetofauna of Belize is relatively well known. Amphibians and reptiles of this country have

been the focus of several major inventory-based studies, the first published more than 60 years ago (Schmidt, 1941), and a considerable wealth of

information has also accumulated on patterns of species distribution, local variation, and natural history (summarized in Lee, 1996, 2000; Stafford and Meyer, 2000). Herpetological investigations in the Guatemalan department of El Petén, with which Belize shares its western border and has greatest faunal affinity, have been similarly extensive (see Campbell and Vannini, 1989; Lee, 1996; Campbell, 1998b). Given this history of attention it is probable that relatively few species of amphibians and reptiles remain to be discovered in the Belize/Petén area. Additional new forms, however, continue to emerge from time to time (e.g., Campbell et al., 1994; Mendelson, 1994; Campbell and Smith, 1997), and from a herpetological perspective, there are still many parts of the region that have yet to be explored.

Small cryptozoic snakes are particularly notable for their ability to escape detection, illustrated within the last few years by the discovery of several new species of *Tantilla* in the *taeniata* group (Campbell and Smith, 1997; Campbell, 1998a; Wilson et al., 1999). Of the 17 species currently recognized within this group (exclusive of the form described here), more than half have been described since 1971, and at least half remain known from fewer than a dozen specimens, providing some indication of the difficulties in finding these snakes (Campbell and Smith, 1997). During recent fieldwork in the Vaca Plateau area of southwestern Belize, another snake of the *Tantilla taeniata* group was found that, although bearing clear resemblance to a species described from Guatemala, *T. impensa* (Campbell, 1998a), differs from that taxon in a number of prominent features. In attempting to determine the status of the specimen I compared it with representative material of *impensa*, as well as examples of other similar species within the *taeniata* group (see Appendix 1) and also consulted the detailed descriptions of these snakes provided by Campbell (1998a), Campbell and Smith (1997), Pérez-Higareda et al. (1985), Savitsky and Smith (1971), Wilson (1982, 1983), Wilson and McCranie (1999), Wilson and Meyer (1971), and Wilson et al. (1999). The specimen cannot be allocated to any of the known species and is thus herein considered representative of a new form, which is described below.

MATERIALS AND METHODS

Ventral count methodology follows that of Dowling (1951), and for ease of comparison with similar species, I have adopted the general sequence of character descriptions used by Campbell (1998a) and Campbell and Smith (1997). Abbreviations used are SVL (snout-vent length); TL (tail length); HL (head length, measured from tip of snout to furthest edge of

posterior-most supralabial); HW (head width, measured at angle of jaw); and ED (eye diameter, measured horizontally at is midpoint). All measurements except for SVL and TL were made to the nearest 0.1 mm using digital calipers held under a dissecting microscope. Sex was determined by observation of anatomical structure at the base of the tail through a small ventral incision. Dorsolateral and ventrolateral fields refer to the broad dark-colored areas between the narrow pale middorsal and lateral stripes, and the lateral stripes and ventrals, respectively.

Affinities of the new form in relation to species with similar characteristics were assessed using nonmetric multidimensional scaling, based on data collected from specimens and selected literature records (Campbell, 1998a; Wilson and McCranie, 1999). Values for each character were standardized before analysis to Z-scores with a mean of 0 and standard deviation of 1, and the ordination of specimens along two NMDS dimensions was plotted. A two-dimensional NMDS solution was sought because the alternative hypothesis suspected the existence of three similarity-based groupings.

Tantilla hendersoni sp. nov. Figures 1–3

Holotype.—The Natural History Museum, London (BMNH) 2002.3 (field PJS 0242); a female from 0.5 km east of Las Cuevas on trail to Monkey Tail River, Cayo District (GR 1643'95"N, 8859'17"W), collected by P. Stafford, S. McMurry, and T. Rainwater on 13 September 2002. This locality (site of the Natural History Museum's field research station) lies in an area of semievergreen broadleaf forest at 580 m.

Diagnosis.—A species of the *T. taeniata* group that may be distinguished from all other members of the genus by having (1) a dark gray-brown, almost black ground color; (2) a pale nape band that is complete medially; (3) a mid-dorsal stripe confined to the vertebral scale row and extending to the distal portion of the tail; (4) narrow pale lateral stripes occupying adjacent thirds of scale rows 3 and 4 that extend to the tip of the tail; (5) the lower third of the paraventral scale row mostly unpigmented; (6) dark mottling on the lateral edges of the ventrals; and (7) 153 ventrals and 64 subcaudals (excluding terminal spine) in the single known female. This species is compared with other regional members of the *taeniata* group in Table 1 and 2, and Figure 4.

Description of Holotype.—A female with an SVL of 207 and TL of 65 mm (tail 23.9% of total length); body attenuate and gracile in form; HL 7.6 mm; HW 5.1 mm; head moderately distinct from neck; snout rounded to somewhat truncate in dorsal view; ED 0.9 mm, about 11.8% of head

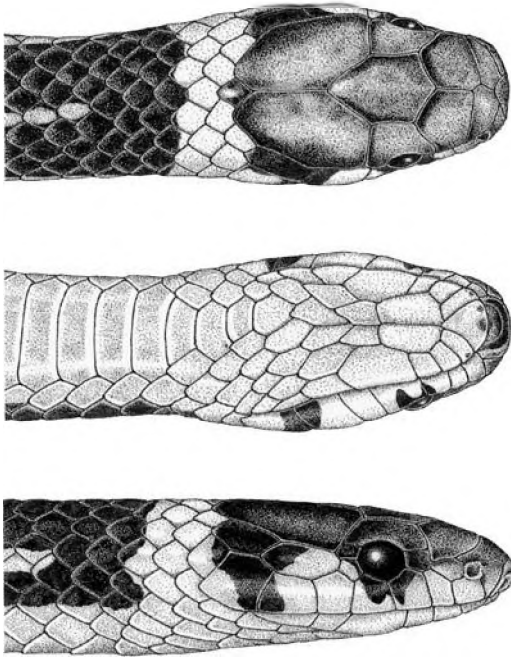


FIG. 1. Dorsal (top), ventral (center) and lateral (bottom) aspects of the head and forebody of BMNH 2002.3. Head length 7.6 mm from tip of snout to furthest edge of posterior-most supralabial.

length and 35% of snout length; pupil subcircular; rostral approximately 1.2 times broader than high; internasals 2.3 times wider than long, laterally in contact with the anterior and posterior nasals; prefrontals large, slightly wider than long, laterally in contact with posterior nasal, second supralabials (right side only), and preocular; median prefrontal suture 0.3 times as long as frontal; frontal approximately 1.5 times longer than wide; parietals 1.7 times longer than wide, median suture 0.6 of frontal length; nasals completely divided, nostril located mostly in posterior portion of anterior nasal; no loreal; 1/1 preoculars; 2/2 postoculars; temporals 1+1, separating supralabials 5–7 from parietal; supralabials 7/7, first in contact with nasals, second in contact with postnasal and preocular, third in contact with preocular, third and fourth in contact with orbit, fifth and sixth in contact with anterior temporal, and seventh (the largest) in contact with anterior and posterior temporals; mental 1.4 times broader than long, in narrow contact with anterior pair of chinshields; anterior chinshields relatively large, about twice as long as wide; posterior chinshields about half of size of anterior chinshields, separated from first ventral by three gulars and two preventrals; infralabials 6/6, first four pairs in contact with

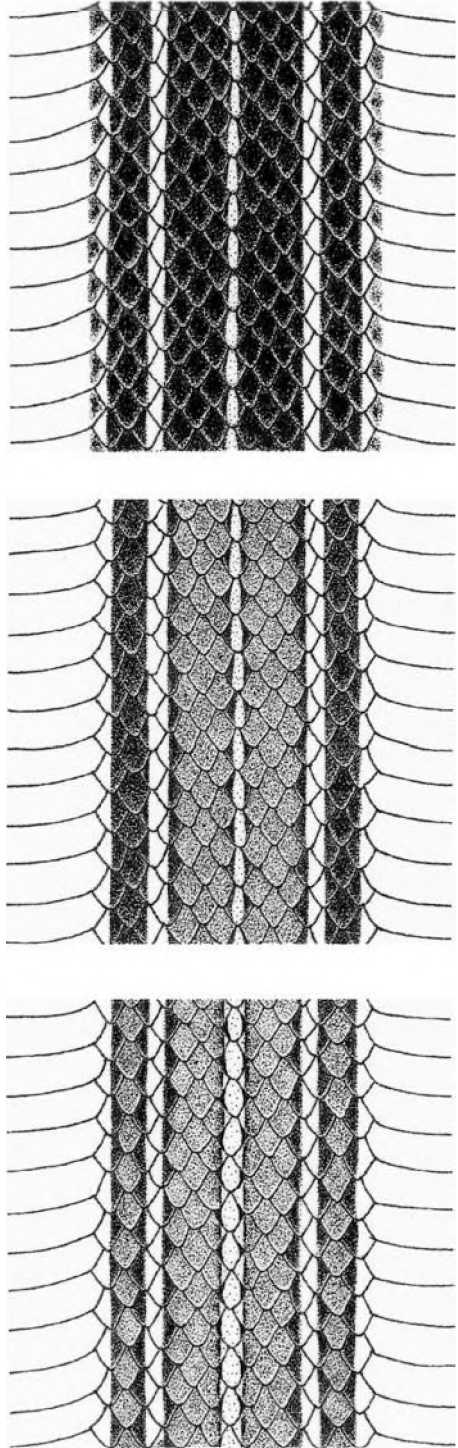


FIG. 2. Midbody pattern characteristics of (from top to bottom) *Tantilla hendersoni* (holotype), *Tantilla impensa* (USNM 523955), and *Tantilla taeniata* (KU 289863).



FIG. 3. Holotype of *Tantilla hendersoni* (BMNH 2002.3), a female 272 mm in total length; tail length 65 mm (Photograph© Frank Greenaway/The Natural History Museum).

anterior chinshields, fourth pair largest; dorsal scales smooth, in 15 longitudinal rows throughout length of body; no apical pits evident; dorsal scales in 6 rows at level of tenth subcaudal; ventrals 153; anal divided; subcaudals 64 (excluding terminal spine), paired.

Ground color in preservative dark gray-brown, almost black; a contrasting pale middorsal stripe arising five scale lengths behind parietals, extending to but less clearly delineated on tail (becoming obscure on distal third); middorsal stripe occupying about median one-half of vertebral scale row; pale lateral stripes on upper third of scale row 3 and lower third of scale row 4, beginning about two scale lengths behind nape band and extending to tip of tail; dark coloration on either side of the pale middorsal stripe (upper two-thirds of scale row 4 to lateral one-quarter of scale row 8) similar to that below pale lateral stripes (lower half of scale row 3, all of 2, and upper two thirds of row 1); lower third of scales on paraventral row pale; lateral edges of ventrals mottled with dark gray, this pigment extending beneath (and visible through) adjacent margins of paraventrals; venter of body and tail otherwise uniformly dull white; dorsal surface of snout pale brown, grading posteriorly to medium brown, with peripheries of major scutes and lateral/posterior edges of

parietals darker; no pale spot on snout; complete pale nape band immediately behind parietals and secondary temporals, nape band 2 dorsal scales long, slightly constricted medially, cream in color grading at level of venter to whitish; on side of head, an area of light pigment covering first and second supralabials, adjacent portions of third supralabial and posterior nasal, this marking continuous along lip margin beneath eye with similar postorbital "spot" involving fifth supralabial, adjacent portions of fourth and sixth supralabials, lower postocular, and anterior temporal; circumorbital area blackish brown, this color extending ventrally as inverted fork-shaped mark on adjacent portions of supralabials 3 and 4 and posteriorly through upper postocular to merge with similar dark pigment on parietal; light postorbital marking and nape band separated laterally by dark gray-brown, extending to lip margin; infralabials immaculate, except for small grayish blotches along outer edge of mental and first two pairs of infralabials; venter of body and tail cream with dark gray-brown mottling on lateral edges of ventrals, this pigment appearing first on scale 13 and increasing in measure toward the tail.

In life, the pale middorsal stripe was orange tan, the pale lateral stripes were yellowish white,

Table 1. Characters used for multidimensional scaling analysis of specimens in the *taeniata* group of *Tantilla*, based on data collected from specimens and selected literature records (Campbell, 1998a; Wilson and McCranie, 1999).

1. Ventral scales
2. Subcaudal scales
3. Snout color (0 = not obviously paler than head; 1 = paler than head)
4. Condition of pale nape band (0 = complete; 1 = interrupted medially)
5. Condition of pale vertebral stripe (0 = confined to median area of vertebral scale row; 1 = inclusive of vertebral scale row and adjacent portions of paravertebral row)
6. Pale vertebral stripe bordered laterally with dark pigment (0 = yes; 1 = no)
7. Pale lateral stripe extending to distal portion of tail (0 = yes; 1 = no)
8. Pale lateral stripe bordered above by dark pigment (0 = yes; 1 = no)
9. Color of dark dorsolateral vs ventrolateral field (0 = distinctly paler; 1 = similar)
10. Dark mottling on lateral edges of ventrals (0 = present; 1 = absent)
11. Color of venter in life (0 = white; 1 = orange/salmon)

and the pale nape band was bright yellow, all of these markings contrasting sharply with the blackish brown color of the dorsolateral and ventrolateral areas. The dorsal surface of the head was pale brown anteriorly, grading on the posterior cranial scutes to medium brown, the peripheries of these scales notably darker; the light-colored areas on the side of the head were yellow; the mental, infralabials, and margins of adjacent chinshields were also yellow. Except for the dark mottling on the lateral edges of the ventrals, the venter was pearl white and semi-translucent. The tongue was dark brown at its tip, grading posteriorly to pale reddish brown. The iris of the eye was uniformly black.

There are 14 stout, distally compressed teeth on the left maxillary. The anterior 12 are relatively small, increase in size posteriorly, and are separated from the last two (these somewhat enlarged) by a small diastema.

Morphometric Analysis.—An ordination plot of character traits in 12 specimens of the *T. taeniata* group based on multidimensional scaling reveals the existence of three distinct clusters (Table 1, Fig. 4). These correspond to *T. hendersoni* and the two species it most closely resembles, *T. impensa* and *T. taeniata*. Separation along the first dimensional axis relates mostly to differences between the specimens in snout color, width of the pale vertebral stripe, pattern characteristics of the dorsolateral and ventrolateral fields, presence/absence of dark mottling on the lateral edges of the ventrals, and coloration of the venter. The second dimension primarily separates *hendersoni* from the specimens of *impensa*. Separation along this axis is related to differences in the number of ventral scales, coloration of the dorsolateral field, and presence/absence of dark mottling on the lateral edges of the ventrals.

Etymology.—The specific name is a patronym in honor of Robert W. Henderson, Curator of Herpetology at the Milwaukee Public Museum,

in recognition of his many published studies on the herpetofauna of Belize.

Distribution.—*Tantilla hendersoni* is known only from the type locality. This lies in an area of distinctive karst topography noted for its many sinkholes and extensive underground cave systems. Las Cuevas itself is named for its proximity to a large subterranean cavern. The limestone forests in the area are continuous with similar formations in the southern Vaca Plateau, Maya Mountains, and adjacent Petén region of Guatemala, over parts of which the range of *T. hendersoni* is likely to extend.

Ecological Notes.—Within the life zone classification system of Holdridge (1967), Las Cuevas lies in a transitional zone between Subtropical Wet and Subtropical Moist Forest. Vegetation in the area is characterized by seasonal broadleaf forest (Penn et al., 2003), with an approximate canopy height of 20–30 m and a relatively open understory predominated by vines and dwarf palms (*Chamaedorea* spp.). Common tree species include *Brosimum alicastrum*, *Manilkara chicle*, *Dialium guianense*, *Cameraria latifolia*, *Sabal mauritiformis*, *Calophyllum brasiliense* var. *rekoii*, and *Coccoloba belizensis*. Average rainfall for the type locality based on incomplete records available for the period 1995–1999 is estimated at 2650 mm per year (N. Garwood, unpubl. data), with most (> 70%) falling between June and December.

No other member of the *T. taeniata* group is known from the collection site of *T. hendersoni* or elsewhere in southern Belize. To the northeast in the provincial districts of Corozal and Orange Walk, there are several records of *T. cuniculator* (Stafford and Meyer, 2000), and this species also occurs at localities in eastern Petén (Lee, 1996; Campbell, 1998b), but it appears to be an essentially lowland form (< 100 m) restricted to less mesic habitats. Given that *hendersoni* has remained unknown in the area for so long, despite the use of methods that have resulted in the detection of various other small leaf litter

Table 2. Comparative features and distribution of snakes of the *Tantilla taeniata* group from Belize and eastern Guatemala. Includes data from Campbell (1998a), Wilson and McCranie (1999), and other selected literature records. *based on an individual from Depto. Yoro, Honduras (UMMZ 58417); although higher than might normally be expected, Wilson and McCranie (1999) found no reason to consider this specimen as other than a representative of *taeniata*.

Character	<i>T. canticular</i>	<i>T. hendersoni</i>	<i>T. impensa</i>	<i>T. taeniata</i>	<i>T. texta</i>
Pale spot on snout	Yes	No	No	No, but snout relatively pale	Yes
Condition of pale nape band	Complete	Complete	Complete or interrupted dorsally	Complete or occasionally interrupted dorsally	Complete
Pale middorsal stripe	Usually absent; sometimes faintly indicated on anterior body	Well defined; confined to vertebral scale row, extending onto tail	Well defined; confined to vertebral scale row; extending onto tail	Well defined, involving vertebral scale row and adjacent thirds of paravertebral rows	Narrow, occupying median third of vertebral scale row and indistinct posteriorly
Dark edging of pale middorsal stripe	Absent	Absent/not discernible	On lateral edges of scales in vertebral row, forming series of dashes	On lateral edges of scales in vertebral and/or paravertebral rows, forming continuous line	On lateral edges of scales in vertebral row
Pale lateral stripe on scale rows 3-4	Narrow, often confined to upper portion of scale row 3; on posterior portion of body	On adjacent thirds of scale rows; extending to tip of tail	On adjacent halves of scale rows; extending to distal portion of tail	On adjacent halves of scale rows; extending to distal portion of tail	On upper two-thirds of row 4 and lower row of 3; extending to distal portion of tail
Pale lateral stripe bounded above and/or below by dark pigment	Yes, below	No/not discernible	Yes, above/both	Yes, both	Yes, both
Color of dark dorsolateral vs. ventrolateral fields	Paler	Similar	Paler/occasionally similar	Similar/paler	Paler
Lower portion of paraventral scales	Darkly mottled	Mostly unpigmented	Unpigmented	Unpigmented	Darkly mottled
Lateral edges of ventrals	Unpigmented	Darkly mottled	Unpigmented	Usually unpigmented, but occasionally with small dark spots	Darkly mottled
Color of venter (in life)	Reddish orange	White	White	Pale purplish pink anteriorly, grading to salmon	Unknown
Ventrals:					
Males	139-145	—	162-165	143-153	—
Females	140-154	153	164-172	139-161(178*)	148

TABLE 2. Continued.

Character	<i>T. cuniculator</i>	<i>T. hendersoni</i>	<i>T. impensa</i>	<i>T. taeniata</i>	<i>T. tecta</i>
Subcaudals:					
Males	53–58	—	68–72	63–70	—
Females	48–53	64	65–72	62–70	54
Tail/Total Length ratio (%)	19.7–22.9	23.9	21–25	22–27.1	23
Maximum known total length (mm)	220 (female)	272 (female)	ca. 725 (female)	415 (female)	222 (male)
Geographic range	N Guatemala and Yucatan Peninsula	SW Belize (including Maya Mts?); possibly also E Guatemala	E Chiapas through central highlands of Guatemala to NW Honduras	Antigua Basin and SE highlands of Guatemala through Honduras to El Salvador and N Nicaragua	NE Petén, Guatemala
Ecological distribution	Tropical dry forest; near sea level to 100 m	Subtropical Moist/Wet forest; 580 m	Tropical and subtropical wet forest; near sea level to 1600 m	Tropical Moist/Dry Forest; 200–1550 m	Tropical dry forest; 220 m

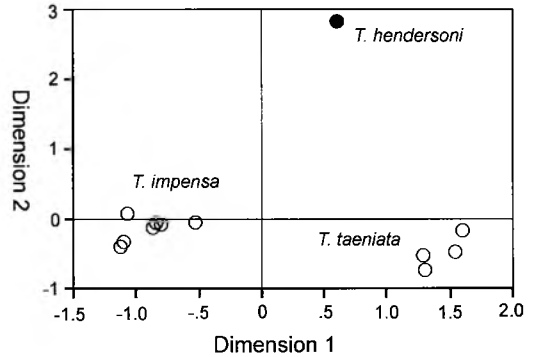


FIG. 4. Ordination of specimens of *Tantilla hendersoni* ($N = 1$), *Tantilla impensa* (7), and *Tantilla taeniata* (4) based on results of multidimensional scaling analysis (Euclidean distance model). For details of characters used, see Table 1.

snakes (intensive microhabitat surveys, drift fence and pitfall trap systems), it is likely to be a rare or at least uncommon species. The specimen was found crawling at the side of a muddy trail through dense forest at 2015 h, within a few meters of a small mussurana (*Clelia clelia*). A fecal deposit produced shortly after capture contained the fragmentary remains of a centipede.

DISCUSSION

Comparisons.—Wilson and Meyer (1971) recognized two sections within the *taeniata* group of *Tantilla* based on differences between the species in dorsal color pattern, the *reticulata* section, consisting of *Tantilla flavilineata*, *Tantilla oaxacae*, and *Tantilla reticulata* and the *taeniata* section (subsequently redefined by Wilson, 1983), to which *Tantilla briggsi*, *Tantilla cuniculator*, *T. impensa*, *Tantilla jani*, *Tantilla johnsoni*, *Tantilla slavensi*, *Tantilla striata*, *T. taeniata*, *Tantilla tayrae*, *Tantilla tecta*, *Tantilla tritaeniata*, *Tantilla trilineata*, *Tantilla triseriata*, and *Tantilla vulcani* can be allocated. In having a pale lateral stripe on scale rows 3 and 4, *T. hendersoni* is associated nominally with the latter section; the pale lateral stripe in *T. flavilineata* and *T. oaxacae* is wider, occupying scale row 4 and adjacent portions of rows 3 and 5, whereas in *T. reticulata* scale row 4 and adjacent portions of rows 3 and 5 are brown. *Tantilla flavilineata* and *T. oaxacae* further differ from *T. hendersoni* in having fewer subcaudals in both sexes (43–52 and 46–52, respectively, vs. 64).

Tantilla hendersoni differs from all other species in the *T. taeniata* group except *T. impensa*, *T. jani*, *T. slavensi*, and *T. tecta* in having a narrow pale middorsal stripe con-

finned to the central area of the vertebral scale row. In *T. briggsi*, *T. cuniculator*, *T. tayrae*, and *T. vulcani*, the pale middorsal stripe is absent, ill-defined posteriorly, or reduced to a series of spots, whereas in the remaining species it is expanded laterally to include all of the vertebral scale row and adjacent portions of the paravertebral rows. The pale lateral stripe in *T. impensa*, *T. jani*, *T. slavensi*, and *T. tecta* is distinctly bordered above (and in *T. jani*, *T. slavensi*, and *T. tecta* also below) by dark flecking or a narrow, continuous dark line, and in these species the color of the dorsum either side of the middorsal stripe is also somewhat paler. *Tantilla jani* may be further distinguished from *T. hendersoni* in having less distinct pale lateral stripes that usually terminate on the posterior section of the body, a nape band that is reduced to a pair of pale spots, a smaller light postorbital marking confined mostly to the fifth supralabial, the first pair of infralabials usually in contact, and fewer segmental counts (females with 143–147 ventrals and 44–47 subcaudals vs. 153 + 64 in the female holotype of *T. hendersoni*). *Tantilla slavensi* further differs from *T. hendersoni* in having a pale nape band that is interrupted medially (vs. complete) and no more than one dorsal scale in length (vs. two in *T. hendersoni*), a pale lateral stripe that is indistinct on the tail (vs. evident even at tip of tail), an orange venter in life (vs. pearl white), and 52–56 subcaudals (vs. 64 in *T. hendersoni*). In *T. tecta*, the snout is marked with a pale spot involving the upper portion of the rostral, internasals, and anterior two-thirds of the prefrontals, the middorsal pale stripe is ill-defined posteriorly, and there are fewer ventrals and subcaudals (148 + 54 in the single known female).

Ventral and subcaudal scale counts in *T. hendersoni* fall directly within the range of *T. taeniata*, to which the new form also bears resemblance in aspects of proportion and general habitus. As indicated by the ordination pattern in Figure 4, however, it is perhaps most closely related to *T. impensa*. This species has a comparable number of subcaudals (65–72 in females vs. 64 in the holotype of *T. hendersoni*), a similarly narrow middorsal stripe that is confined to the central area of the vertebral scale row and extends onto the distal portion of the tail, and a dark ventrolateral field. In *T. impensa* however, the dark ground color on either side of the middorsal stripe is typically paler than that below the lateral stripe (Fig. 2) and bordered above and below by dark gray-brown, the lateral edges of the ventrals are unpigmented, and females have a higher number of ventrals (164–172 vs. 153 in *T. hendersoni*). *Tantilla impensa* is potentially also a larger species, with females attaining total lengths in excess of 720 mm (Campbell, 1998a).

As presently defined, the range of *T. impensa* extends from eastern Chiapas, Mexico, across the northern slopes and foothills of eastern Guatemala (Montañas del Mico, Sierra del Merendón, Sierra del Espíritu Santo to northwest portion of Sierra de Los Cuchumatanes) to western Honduras (Wilson and McCranie, 1999), thus placing it within considerable geographic proximity to the new form described here. The two species also appear similar in their ecological distribution, *T. impensa* having been recorded from Tropical and Subtropical Wet forest formations at elevations from near sea level to 1600 m. The evident distinctions between *T. impensa* and *T. hendersoni* in color pattern and ventral scale numbers, however, suggest that they are not simply representatives of different populations of the same species, a conclusion further supported by the fact that geographic variation in *T. impensa* appears to be low; throughout its range, the pale nape band in *T. impensa* may be either complete or interrupted dorsally (Campbell, 1998a; Wilson and McCranie, 1999), and in SMF 79114 from Depto. de Copán, Honduras (a small juvenile with lower body and tail missing), the dorsolateral coloration is exceptionally dark, but in the nature of striping and all other diagnostic elements of color pattern this species appears to be relatively stable.

Four additional species of *Tantilla* occur in the area of Belize with which *T. hendersoni* is broadly sympatric and may be confused; *Tantilla cuniculator*, *Tantilla moesta*, *Tantilla schistosa*, and *Tantilla tecta*. *Tantilla cuniculator* has a brown dorsum with usually no evidence of a middorsal stripe, a pale nape band that is orange-brown in color and involves the posterior tips of the parietals, a pale yellow-orange spot on the snout, a reddish orange venter, and fewer subcaudals (48–53). *Tantilla moesta* has a longer pale nape band that extends posteriorly from the parietals for a length of at least three dorsal scales and usually includes the posterior-most three supralabials. In this species, the dorsum and venter are also uniformly dark brown or black, and there are no longitudinal stripes. *Tantilla schistosa* has a uniformly olive-colored or reddish brown dorsum, a pale nape band that involves the posterior portions of the parietals, 20–40 subcaudals, and a relative tail length of 12.8–20.1% (vs. 23.9% in the holotype of *T. hendersoni*). *Tantilla tecta* is known from a single locality in northeastern Petén (Campbell and Smith, 1997) and differs in having a pale spot on the snout, enclosing the upper portion of the rostral, internasals and anterior two-thirds of the prefrontals, a pale middorsal stripe that is indistinct on the lower body, and 148 ventrals and 54 subcaudals in the single known female. *Tantillita canula* and *Tantillita lintoni* also occur in Belize, of which *T. lintoni*

has been further reported from the same specific locality (Stafford and Meyer, 2000). These species are easily distinguishable from *T. hendersoni*, however, in lacking a pale nape band and lateral stripes, and in having the middorsal stripe (if present) usually reduced to a series of spots posteriorly.

Several species of *Tantilla* to which *T. hendersoni* is ostensibly related are known from only a few specimens or, as in the similar case of *T. tecta*, only the holotype. Consequently, there is no possibility of assessing variation in the traits deemed to be distinctive of these forms, a number of which resemble one another closely and have been described from a fairly limited area. But the alternative—to wait until comparative material becomes available—is not practical when dealing with such infrequently collected (and possibly rare) species. Clearly, a pressing need exists for detailed systematic studies on the *T. taeniata* group of *Tantilla*, and molecular techniques may be of particular benefit in elucidating relationships among these snakes.

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APPENDIX 1

Specimens Examined

Tantilla cuniculator: Belize: Tower Hill, Orange Walk District (MPM 7608). Mexico: 9.7 km SE Coba, Quintana Roo, 0 m (KU 171745). *Tantilla impensa*: Honduras: Quebrada Grande, Depto. de Copán, 1600 m (FMNH 236413; USNM 523955); Quebrada Grande, Depto. de Copán, 1300 m (SMF 79114); Lago de Yojoa, Depto. de

Cortés (USNM 523956). Guatemala: Livingston, Punta Cocoli, Izabal, 2 m (UTA 39550, paratype); Los Amates, Aldea Vista Hermosa, Izabal, 650 m (KU 191103); Los Amates, Sierra del Espíritu Santo, approximately 1 km NE Aldea San Antonio, Izabal, approximately 660 m (UTA 28532, paratype). *Tantilla jani*: Guatemala: no specific locality (BMNH 1946.1.8.68, lectotype).

Tantilla taeniata: El Salvador: Usulután, Cerro del Tigre, 1100 m (KU 289863). Guatemala: no specific locality (FMNH 40890); Parque Nacional Laguna El Pino, Santa Rosa (UTA 22848).

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A New Species of *Echinosaura* (Squamata: Gymnophthalmidae) from Ecuador

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ABSTRACT.—A new species of *Echinosaura*, *Echinosaura brachycephala*, is described from two localities on the Pacific versant of the Ecuadorian Andes. The new species differs from all other species of the genus by its conspicuously short head with a high domed snout in lateral profile and various scalation characteristics including the number of ventral scales per caudal segment, the arrangement of dorsal body scales, and a reduced or absent postmental scale. A key to the species of *Echinosaura* and *Teuchocercus* is provided.

Lizards of the genus *Echinosaura* are small terrestrial “microteiids” that are distributed from western Panama across northwestern Colombia to west-central Ecuador. Although usually found in the vicinity of streams, these lizards live somewhat more terrestrially than the semiaquatic *Neusticurus* (Uzzell, 1965a,b). Although they appear to be predominantly nocturnal (Uzzell 1965a), active *Echinosaura* can be observed during the day as well (Dunn, 1944; Breder, 1946; Uzzell, 1965a). In his revision of *Echinosaura*, Uzzell (1965a) recognized a single species (*Echinosaura horrida*) divided into three subspecies. A few years later, a new genus and species, *Teuchocercus keyi*, presumably related to *Echinosaura*, was described by Fritts and Smith (1969). Recently, Fritts et al. (2002) have described a new species of

Echinosaura and have elevated all three subspecies of *E. horrida* to species. Thus, as currently understood, the genus *Echinosaura* contains four species: *E. horrida* Boulenger, *Echinosaura orcesi* Fritts et al., *Echinosaura palmeri* Boulenger, *Echinosaura panamensis* Barbour.

We examined a rather large series of an apparently undescribed, conspicuously short-headed species of *Echinosaura* from two localities on the Pacific versant of the Ecuadorian Andes. The differences in head shape and some scalation characteristics are so conspicuous that this taxon cannot be confused with any of the known species of *Echinosaura*.

MATERIALS AND METHODS

A list of the specimens examined is provided in Appendix 1. Additional data for *E. orcesi* were taken also from Fritts et al. (2002). Discriminant function analysis (performed with Statistica for

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Table 1. Selected measurements, proportions and scale characters in *Echinosaura brachycephala* (10 males, 15 females), *Echinosaura orcesi* (1 male, 1 female; data also from Fritts et al. 2002), *Echinosaura horrida* (14 males, 13 females), *Echinosaura palmeri* (6 males, 5 females), *Echinosaura panamensis* (5 males, 5 females), and *Teuchocercus keyi* (6 males, 7 females); range is followed by mean value and one standard deviation in parentheses. Abbreviations: HL = head length; HW = head width; SL = snout length; SVL = snout-vent length; Paravertebrals = scales between dorsal paravertebral rows; Postmental = level of first infralabial to which the postmental reaches; Subcaudals = number of ventral scales per caudal segment.

		<i>E. brachycephala</i>	<i>E. orcesi</i>	<i>E. horrida</i>	<i>E. palmeri</i>	<i>E. panamensis</i>	<i>T. keyi</i>
Max. SVL	males	72.0	70.0	86.0	70.0	71.0	80.0
	females	78.0	81.0	80.0	67.0	74.0	64.0
HL/HW	males	1.47–1.59	1.89	1.49–1.79	1.63–1.76	1.41–1.80	1.45–1.51
	females	(1.52 ± 0.04)		(1.65 ± 0.08)	(1.69 ± 0.05)	(1.59 ± 0.13)	(1.50 ± 0.02)
		1.43–1.60	1.93	1.61–1.84	1.82–1.90	1.61–1.90	1.49–1.53
		(1.53 ± 0.04)		(1.73 ± 0.06)	(1.86 ± 0.03)	(1.73 ± 0.10)	(1.51 ± 0.02)
SL/SVL	males	0.067–0.073	0.092	0.071–0.083	0.081–0.094	0.072–0.088	0.070–0.074
		(0.069 ± 0.002)		(0.078 ± 0.003)	(0.088 ± 0.004)	(0.081 ± 0.005)	(0.072 ± 0.002)
	females	0.062–0.071	0.087	0.076–0.083	0.080–0.089	0.077–0.087	0.071–0.075
		(0.065 ± 0.002)		(0.079 ± 0.002)	(0.086 ± 0.003)	(0.083 ± 0.004)	(0.073 ± 0.002)
Internasal		single	single	single	longitudinally divided	longitudinally divided	longitudinally divided
Frontal		single	single	single	single	transversely divided	usually single
Postmental	males	0.0–0.2	ca. 1.0	0.7–1.1	1.2–1.8 (1.40 ± 0.25)	1.0–1.4 (1.18 ± 0.16)	0.4–0.7 (0.53 ± 0.09)
	females	(0.07 ± 0.06)	ca. 1.0	(0.93 ± 0.11)	1.0–2.0 (1.46 ± 0.38)	1.0–1.5 (1.20 ± 0.21)	0.4–0.7 (0.53 ± 0.10)
		0.0–0.3		0.7–1.2			
		(0.12 ± 0.09)		(0.97 ± 0.11)			
Infralabials	males	3 (3.0 ± 0.0)	2–3	3–4 (3.6 ± 0.49)	4–5 (4.3 ± 0.47)	5 (5.0 ± 0.0)	3–4 (3.1 ± 0.32)
	females	3 (3.0 ± 0.0)	2–3	3–4 (3.5 ± 0.50)	4–5 (4.2 ± 0.40)	5 (5.0 ± 0.0)	3–4 (3.1 ± 0.28)
Femoral pores	males	7–9 (8.2 ± 0.60)	14–15	8–9 (8.7 ± 0.45)	7–8 (7.5 ± 0.50)	7–8 (7.2 ± 0.40)	8–11 (9.2 ± 0.96)
	females	1–2 (1.3 ± 0.44)	5–6	1 (1.0 ± 0.0)	0–1 (0.6 ± 0.49)	0–1 (0.2 ± 0.40)	1 (1.0 ± 0.00)
Paravertebrals	males	2–5 (3.8 ± 0.87)	–	0 (0.0 ± 0.0)	4–8 (5.8 ± 1.46)	3–5 (4.2 ± 0.75)	2–4 (3.1 ± 0.31)
	females	4–6 (4.7 ± 0.62)	–	0 (0.0 ± 0.0)	3–6 (5.0 ± 1.26)	3–5 (4.0 ± 0.63)	2–4 (3.2 ± 0.42)
Subcaudals		4	5–6	3	3	3	3

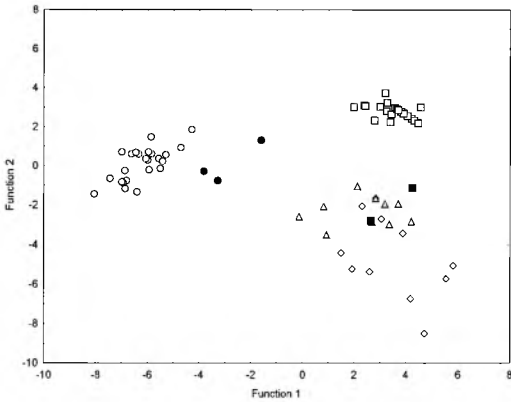


FIG. 1. Discriminant function analysis based on three characters; empty circles: *Echinosaura brachycephala*; empty squares: *Echinosaura horrida*; solid squares: *Echinosaura orcesi*; diamonds: *Echinosaura palmeri*; triangles: *Echinosaura panamensis*, and solid circles: *Teuchocercus keyi*. See text for details.

Windows vers. 6) was used to evaluate the phenetic distinctness of a priori groups (see Appendix 1 for specimens used in this analysis). Nomenclature of dorsal head scales follows Fritts et al. (2002). All measurements were made using precision calipers and were rounded to the nearest 0.1 mm. Head length was measured from the tip of the snout to the anterior margin of the ear opening. Snout length was measured from the tip of the snout to the anterior border of the orbit. Head width was determined as the maximum width of the head. The number of ventral scales per caudal segment (in a longitudinal row) was determined at the seventh caudal segment. Abbreviations for museum collections follow those of Leviton et al. (1985).

RESULTS

A comparison of selected morphometric and scalation characters in the short-headed *Echinosaura*, *E. horrida*, *E. orcesi*, *E. palmeri*, and *E. panamensis*, is provided in Table 1. Nonoverlapping differences between the short-headed *Echinosaura* and the remaining species were observed in the number of ventral scales per caudal segment and the relative size of the postmental scale. Only slightly overlapping ranges were found in the relative snout length (ratio snout length/snout-vent length).

Data from 25 specimens of the short-headed *Echinosaura*, 27 specimens of *E. horrida*, 2 specimens of *E. orcesi*, 11 specimens of *E. palmeri*, 10 specimens of *E. panamensis*, and 3 specimens of *T. keyi* were included in a discriminant function analysis (DFA). Males and females were analyzed together because no statistically significant differences were detected between sexes in the

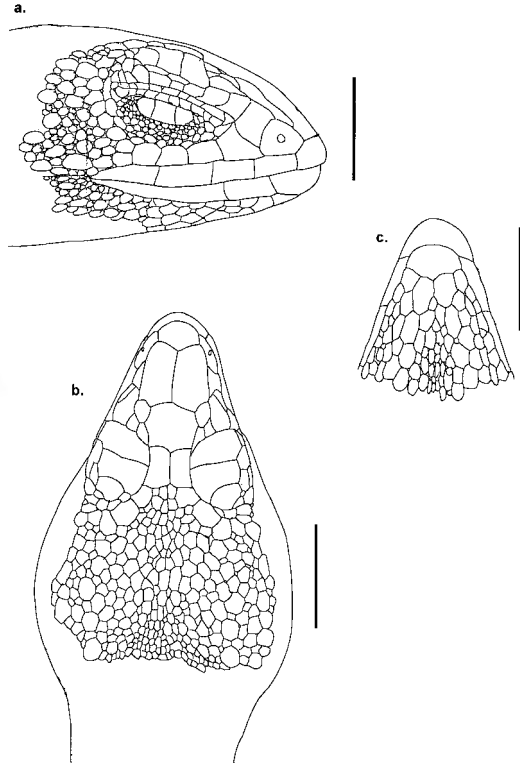


FIG. 2. Head of holotype of *Echinosaura brachycephala* (MHNG 2359.77). (A) Lateral view; (B) dorsal view; (C) ventral view. Scale bars equal 5.0 mm.

included characters. Figure 1 shows the results of a DFA based on the following characters: (1) POSTMENTAL: level of first infralabial to which the postmental reaches (if the postmental did not reach to first infralabial or was absent, it was recorded as zero); (2) SNOUT: ratio snout length/snout-vent length (SVL); and (3) PARAVERTEBRALS: number of scales between paravertebral longitudinal rows of tubercles on dorsum. The first discriminant function (eigenvalue 21.357) was $DS = 0.512 [\text{SNOUT}] + 0.947 [\text{POSTMENTAL}] - 0.607 [\text{PARAVERTEBRALS}]$. The second discriminant function (eigenvalue 7.055) was $DS = -0.447 [\text{SNOUT}] - 0.087 [\text{POSTMENTAL}] - 0.909 [\text{PARAVERTEBRALS}]$. The first and second discriminant functions correctly classified 100% of the Ecuadorian a priori groups but failed to completely separate the specimens of *E. orcesi*, *E. palmeri*, and *E. panamensis*. We describe the short-headed *Echinosaura* as follows.

Echinosaura brachycephala sp. nov.

Holotype.—MHNG 2359.77 (Fig. 2), an adult male, from Las Pampas (= San Francisco de las

Pampas, 0°25'60"S, 78°58'0"W, 1275 m elevation), Provincia Cotopaxi, Ecuador, collected May 1985 by G. Onore.

Paratypes.—MHNG 2359.26, 2359.34–37, 2359.43–44, 2359.51, 2359.53, 2359.56, 2359.62–63, 2359.65–66, 2359.68–72, 2359.74, 2359.76–78, 2359.80, 2359.83–87, 2359.91, 2359.93–94, 2359.98, SMF 81603–04, ZFMK 46370–75, 76376, same collecting data as holotype; MHNG 2360.1, 2360.4A, 2360.11, 2360.14, 2360.28, 2360.30, 2360.34, SMF 81605, from Tandapi (= Manuel Cornejo Astorga, 0°25'0"S, 78°47'60"W, 1665 m elevation), Provincia Pichincha, Ecuador, collected October 1984 by G. Onore; 2360.39, from Tandapi, Provincia Pichincha, Ecuador, collected December 1983 by G. Onore. Most paratypes are adults, except MHNG 2359.70–72, 2359.84–85, 2359.87, 2359.91, 2359.93–94, 2360.1, 2360.4A, 2360.28, 2360.30, and 2360.34, which are juveniles and subadults (SVL less than 55 mm).

Diagnosis.—A medium-sized species (SVL in largest specimen 78.0 mm) of the genus *Echinosauro* that differs from all other species of this genus by the number of ventral scales per caudal segment (four scales per caudal segment in *E. brachycephala* vs. three scales in the other species (except *E. orcesi* which has 5–6 scales per caudal segment) and the relative size of the postmental scale (postmental scale reduced or absent in *E. brachycephala*, not reaching beyond one-third of first infralabial vs. postmental not reduced, always reaching well beyond one-half of first infralabial in the other species). It differs also by its relatively short snout (ratio snout length/SVL 0.06–0.07 in *E. brachycephala* vs. 0.07–0.09 in the other species). It can be readily distinguished from *E. horrida* by its dorsal scalation (2–6 scales between longitudinal rows of tubercles in *E. brachycephala* vs. longitudinal rows of tubercles juxtaposed in *E. horrida*) and the absence of a conspicuous pale band across chin (present in *E. horrida*). *Echinosauro brachycephala* is further differentiated from *E. palmeri* and *E. panamensis* by having a single internasal (divided in *E. palmeri* and *E. panamensis*) and the number of infralabials (three in *E. brachycephala* vs. 4–5 in *E. palmeri* and *E. panamensis*). *Echinosauro brachycephala* can be further distinguished from *Echinosauro orcesi* by having a lower femoral pore count (males: 7–9 in *E. brachycephala* vs. 14–15 in *E. orcesi*; females: 1–2 in *E. brachycephala* vs. 5–6 in *E. orcesi*). Also, *E. orcesi* lacks continuous rows of tubercles in the paravertebral area of the dorsum (present in *E. brachycephala*). *Echinosauro brachycephala* differs from the only species in the presumably closely related genus *Teuchocercus*, *T. keyi*, by its different caudal scalation (tail with only small conical scales in *E. brachycephala* vs. tail bearing conspicuous whorls of spines in *T. keyi*), the number of ventral scales per caudal segment (four scales per

caudal segment in *E. brachycephala* vs. three scales in *T. keyi*) and by the absence of granular scales covering all of the tympanum (present in *T. keyi* although this is variable with adults having more extensive coverage than juveniles but always discernable; in some *E. brachycephala* there are granular scales in the periphery of the tympanum). Also, most *T. keyi* have 2–4 scales separating the paravertebral rows (usually 4–6, rarely two, in *E. brachycephala*), usually paired internasals (single in *E. brachycephala*) and some individuals have prefrontals (absent in most *E. brachycephala*). Most individuals of *T. keyi* have pale markings on the base of the tail (absent in adult *E. brachycephala* but usually present in juveniles).

Description of the Holotype.—Adult male, as indicated by swollen base of tail and number of femoral pores; SVL 68.5 (all measurements in millimeters); tail (complete) length 112.0; axilla to groin distance 29.8; head length 16.8; snout length 4.6; head width 11.4; shank length 10.8; tongue with imbricate scalelike papillae; head scales mostly smooth, some wrinkled or tuberculate and convex, none with numerous longitudinal ridges; rostral scale wider (2.8) than long (1.2), higher than adjacent supralabials, in contact with internasal, nasal and first supralabials posteriorly; internasal single, wider (2.0) than long (1.5), posterior suture angular with point directed posteriorly, in contact with nasals laterally, frontonasals posteriorly; nostril pierced in a single large nasal; nasal posteriorly in contact with frenocular (subrectangular, length 1.1, height 1.3) and lorilabial (subtriangular, length 1.7, maximum height 1.5); a pair of frontonasals (length 3.5, width 1.6), in contact with each other medially (suture length 2.5), in contact with presupraocular scales, frontal posteriorly, and frenocular laterally; frontal single, subhexagonal, longer (2.5) than wide (2.3), anterior suture angular with point directed anteriorly, lateral sutures almost straight, posterior suture angular with point directed posteriorly, in contact with presupraocular scales laterally, first supraocular on left side, frontoparietals posteriorly; a pair of frontoparietals (length 1.9, width 1.0), subrectangular, in contact with each other medially (suture length 1.3), in contact with first and second supraoculars; supraoculars three, third supraocular much smaller than first and second, only the first supraocular in contact with ciliaries; superciliary series complete; transparent area (palpebral disc) in lower eyelid unpigmented, divided by vertical grooves into 3 parts; parietal, interparietal, occipital, and temporal areas with small to medium-sized, polygonal, convex to tuberculate scales; tympanum superficial, pigmented; only slightly recessed in an external auditory meatus; supralabials four; infralabials three; mental wider (3.5) than long (1.5), in contact

with first infralabials, postmental posteriorly; scales on ventral surface of head irregular; postmental wider (2.5) than long (1.4), subpentagonal, posterior suture angular, point directed posteriorly, in contact with first infralabial; genials not differentiated; no gular fold; dorsal and lateral neck scales heterogeneous, conical scales interspaced with smaller, granular scales, cones of upper sides of neck in more or less longitudinal rows; ventral neck scales heterogeneous, larger keeled to low conical scales interspaced with smaller, granular scales; dorsal scales heterogeneous, large tuberculate scales variously disposed, interspaced with smaller, almost granular scales; a pair of paravertebral rows of tubercles, slightly undulating on posterior portion of body, separated by a minimum of two scales in thoracic region, separated by 4–6 scales on most of dorsum; most of ventral scales arranged in obtusely keeled longitudinal and transverse rows; complete transverse ventral scale rows 23 (between levels of axilla and groin); longitudinal ventral scale rows at midbody 8; cloacal plate scales four, medial two much larger than lateral scales; four rows of scales between posteriormost ventral plates and cloacal plates; tail cycloitetragonal, slightly compressed; dorsal and lateral surface of tail with enlarged conical tubercles; these tubercles are scattered irregularly at the base of tail but are arranged regularly (but both longitudinally and transversally disjunct) beginning distal to base of tail where segments are discernable; largest tubercle at the end of each segment, preceded by two gradually decreasing scales in a longitudinal line, but ending 2–3 scale rows before the anterior margin of the preceding caudal segment; anteriormost scales in each caudal segment about the same size as adjacent scales; ventral caudal scales smooth, flat, with 4 subcaudals in one segment (in a longitudinal row).

Limbs pentadactyl; digits clawed; forefoot without enlarged platelike scales along inner margin between thumb and wrist; dorsal and ventral brachial scales polygonal, of varying sizes, keeled to tuberculate; dorsal manus scales polygonal, smooth, subimbricate; palmar scales small, polygonal, smooth; dorsal scales on fingers single (except on proximal portion of fourth finger) smooth, quadrangular, covering dorsal half of digit, overhanging subdigital scales, four on I, seven on II, 10 on III, 12/11 on IV, six on V; subdigital scales smooth, in single series, 6/7 on I, 11 on II, 17/16 on III, 16 on IV, 10/12 on V; anterodorsal thigh scales heterogeneous, enlarged keeled scales interspaced with smaller, granular scales; ventral thigh scales more or less homogeneous, smooth, subimbricate; femoral pores 8/9; six scales between medial-

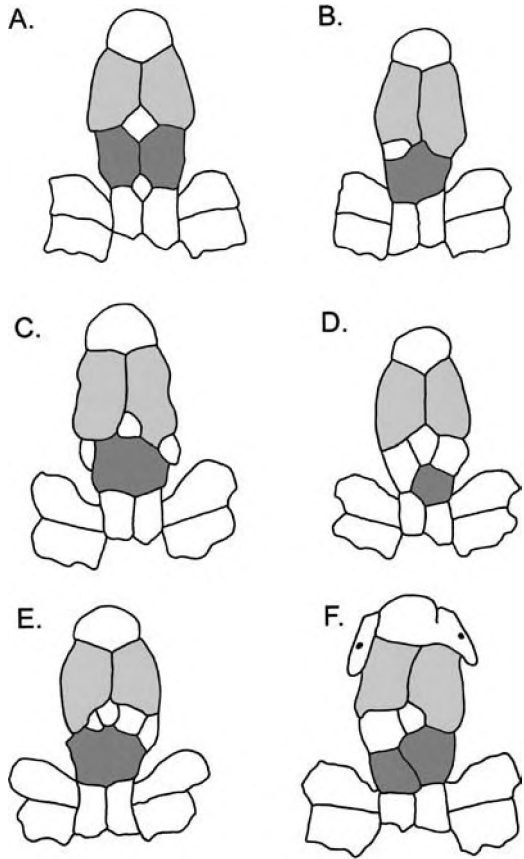


FIG. 3. Variation in dorsal head scales in the type series of *Echinosauro brachycephala*. (A) MHNG 2359.63; (B) MHNG 2359.26; (C) MHNG 2359.98; (D) MHNG 2360.14; (E) MHNG 2359.37; (F) SMF 81603. Frontonasals with light shading and frontals with dark shading.

most femoral pores; anterior and anteromedial pes scales polygonal, subimbricate, smooth, irregular in size with the largest scales distally; scales on dorsal surface of digits single (except on proximal portions of toes III–V), quadrangular, smooth, overhanging subdigital scales, 5/4 on I, 8/7 on II, 15 on III, 24/23 on IV, 14 on V; subdigital scales single, eight on I, 13 on II, 20/19 on III, 26 on IV, 19 on V.

Coloration in Preservative (70% Ethanol).—Dorsal surfaces of head, body and tail uniform; lateral body brown with six (right) and four (left) vague pale brown round blotches; lateral head dark brown with some vertical pale brown streaks reaching onto labials; lower surface of head pale brown with a few dark brown spots; belly irregularly checkered with dark and pale brown; ventral surfaces of limbs and tail pale

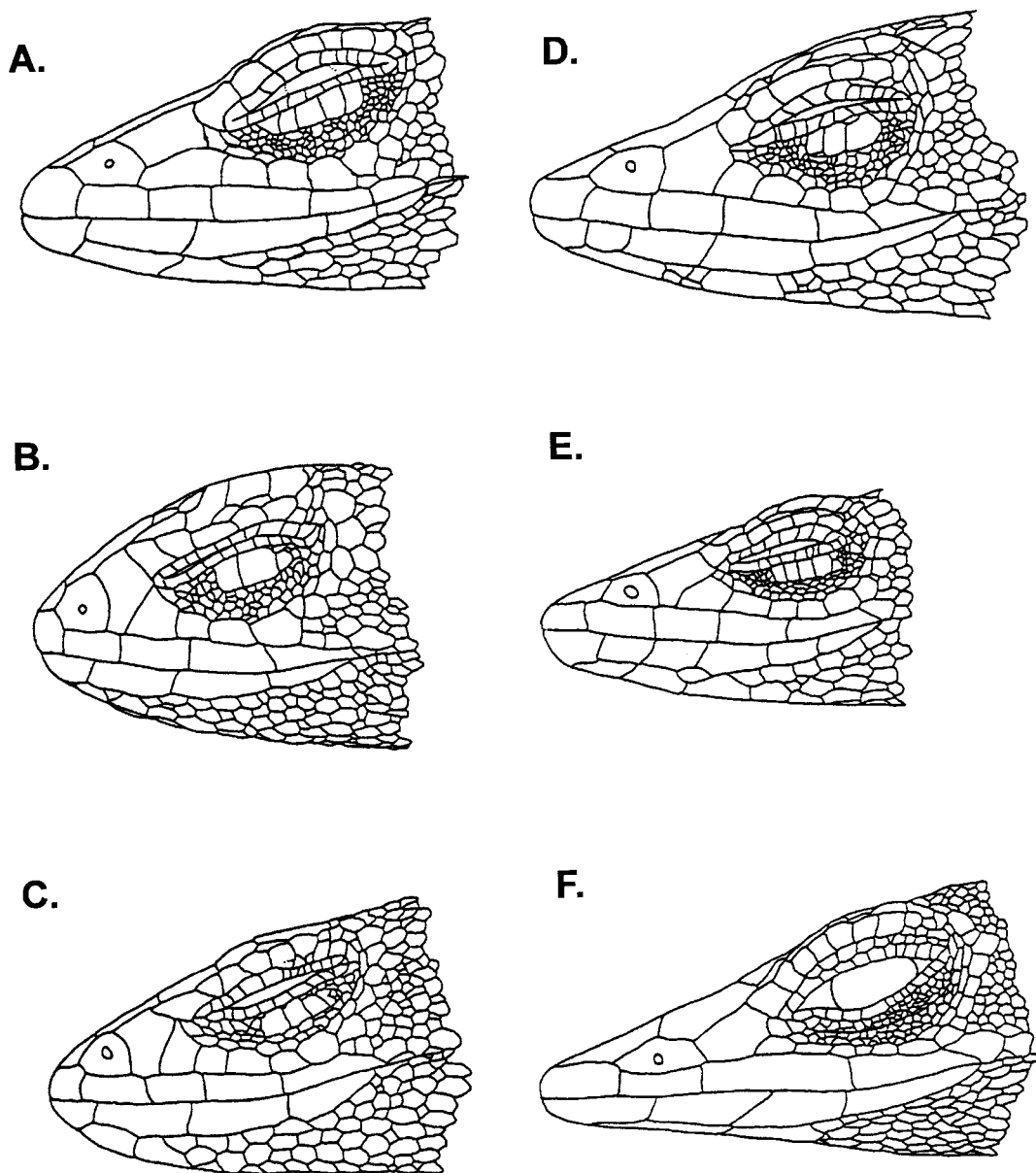
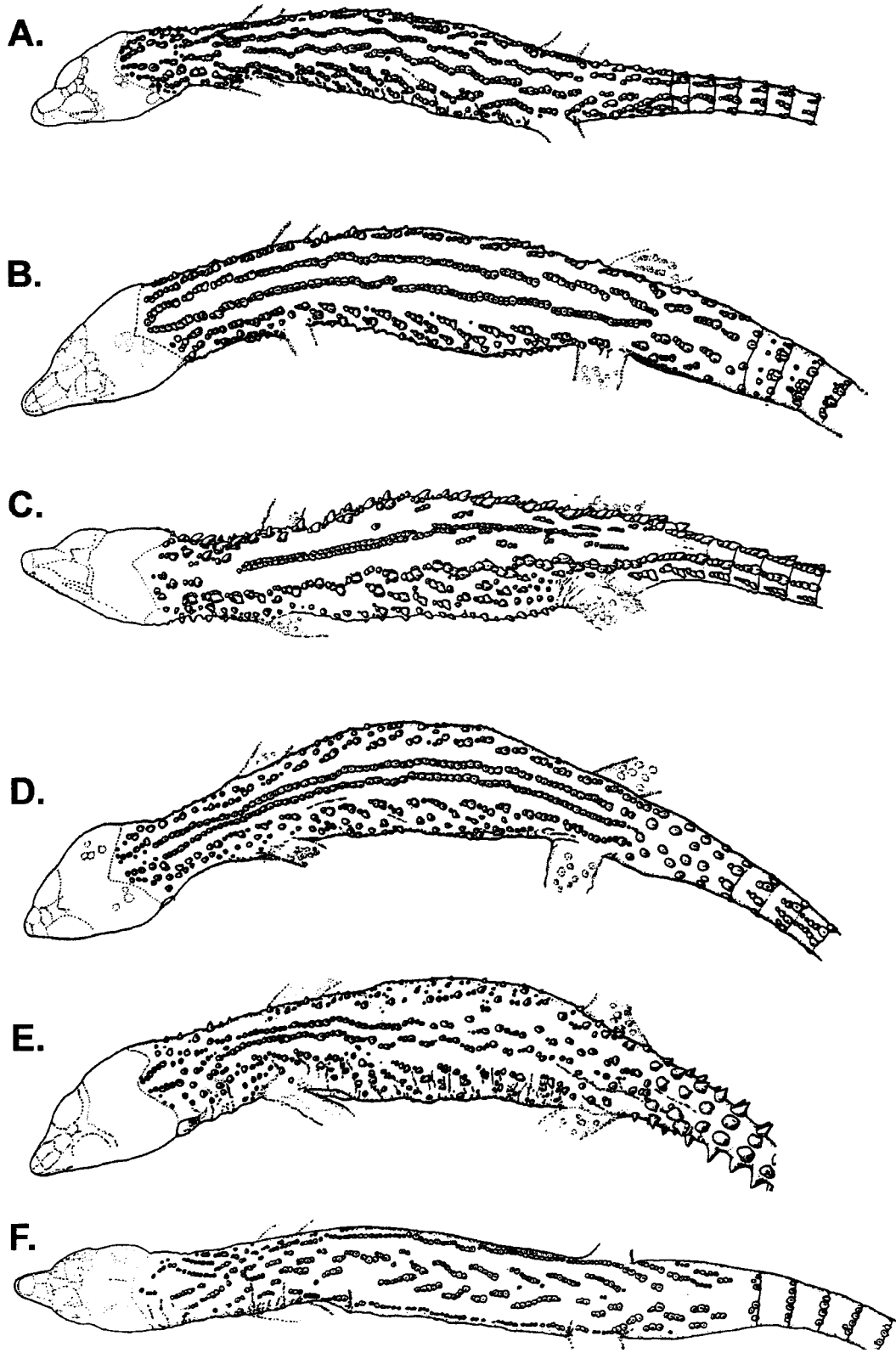


FIG. 4. Lateral view of head. (A) *Echinosauro horrida* (ZFMK 43768); (B) *Echinosauro brachycephala* (ZFMK 46371); (C) *Teuchocercus keyi* (MHNG 2284.59); (D) *Echinosauro palmeri* (BMNH 1923.10.12.14); (E) *Echinosauro panamensis* (ZFMK 49107); (F) *Echinosauro orcesi* (NMW F 3087). Drawings by Mathias Günther.

brown with dark brown mottling; palmar and plantar surfaces pale brown.

Variation.—The paratypes agree well with the holotype in all characters. Most variation is observed in dorsal head scalation (Fig. 3). Although all specimens have a single internasal and a pair of frontonasals, there is considerable variation in the frontal and prefrontal region. Twelve of 41 specimens (29.3%) have the frontal

longitudinally divided. There is a single unpaired scale centrally between the frontonasals and the frontal in six of 41 specimens (14.6%). Two of these specimens have an additional scale between the frontal and the frontoparietals. In three of 41 specimens (7.3%), there are 1–3 irregular scales (“prefrontals”) between the frontonasals and the frontal, and in two specimens, there are three relatively symmetri-



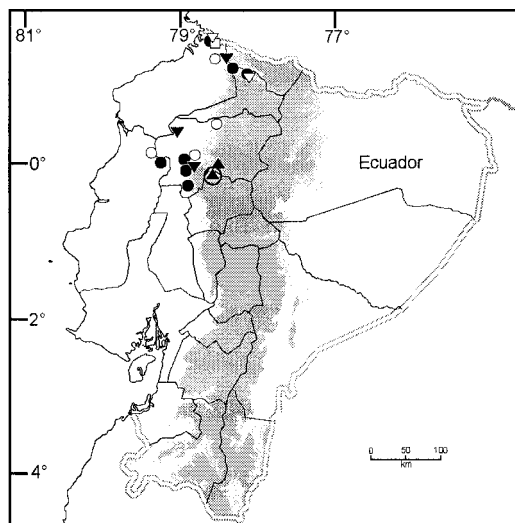


FIG. 6. Distribution of the Ecuadorian species of *Echinosauro*. *Echinosauro brachycephala* (triangles; type locality encircled), *Echinosauro horrida* (circles), *Echinosauro orcesi* (squares), and *Teuchocercus keyi* (inverted triangles). Open symbols represent literature records (Fritts et al., 2002). Pale shading indicates elevations above 1000 m; darker shading indicates elevations above 2000 m.

cal scales ("prefrontals") between the frontonasals and the frontal. In one specimen (SMF 81603), the internasal is fused with the left nasal (Fig. 3F). The range for relative tail length (ratio tail length/SVL) is 1.62–1.80. Supralabials are 3–5 (mostly 4), infralabials are constantly three. Subdigital lamellae on the fourth finger are 16–23, on the fourth toes 23–32. See Table 1 for variation in selected measurements and proportions and scale characters in the type series.

Variation in coloration is minimal. Most juveniles and subadults (SVL less than 55 mm) have a more or less conspicuous pair of pale brown blotches on the dorsal surface of the base of tail. These pale markings obviously disappear with age, and only two of the adults examined (MHNG 2359.76, SVL 62.0 mm; MHNG 2359.65, SVL 60.0 mm) have more or less distinct pale brown blotches at the base of tail. The smallest specimen examined is MHNG 2359.71 (SVL 34.0 mm).

Etymology.—The species name is derived the Greek *brachy*, meaning "short" and the Greek

cephal, meaning "head" in reference to the conspicuously short head of this species.

DISCUSSION

The relationships of *E. brachycephala* remain unclear. Its head shape (especially in lateral view) is much more similar to that of *T. keyi* than to that of the other species of *Echinosauro* (see Fig. 4). There is a general north south trend in respect of relative snout length. The Panamanian and Colombian species (i.e., *E. orcesi*, *E. palmeri*, and *E. panamensis*) have markedly longer snouts than *E. brachycephala*, *E. horrida*, and *T. keyi* from Ecuador. However, in dorsal scalation *E. brachycephala* resembles *E. palmeri* and *E. panamensis* more than the geographically closer *E. horrida* (see Fig. 5). We strongly agree with Fritts et al. (2002) that *palmeri* and *panamensis* should be treated as separate species rather than subspecies of *E. horrida* as did Uzzell (1965a). The strikingly different tail morphology of *T. keyi* is obviously an autapomorphic character. Further studies are needed to evaluate the relationships of the species currently placed in *Echinosauro* and *Teuchocercus*.

Echinosauro horrida and *T. keyi* have broadly overlapping geographic ranges (Fig. 6). In the vicinity of Mataje (330 m elevation, Esmeraldas Province), three of the species in question (*E. orcesi*, *E. horrida*, and *T. keyi*) appear to occur sympatrically, and at Paramba (770 m elevation, Imbabura Province), both *E. horrida* and *T. keyi* have been collected (Fritts et al., 2002; also data from specimens examined by authors). *Echinosauro brachycephala*, however, is currently known only from the foothills of the Andes and appears to have an allopatric distribution relative to *T. keyi* and the other species of *Echinosauro*. The documented elevational ranges of the species of *Echinosauro* and *Teuchocercus* are *E. brachycephala* (1275–1665 m), *E. orcesi* (250–820 m), *E. horrida* (200–860 m), *E. palmeri* (30–1520 m), *E. panamensis* (560–909 m), and *T. keyi* (280–860 m) (Fritts et al., 2002; also data from specimens examined by authors). Thus, *E. brachycephala* occurs at higher elevations as *E. horrida* and *T. keyi*.

KEY TO THE SPECIES OF *Echinosauro* AND *Teuchocercus*

- 1a. Four ventral scales per caudal segment; postmental scale reduced or absent, not reaching beyond one-third of first infralabial *Echinosauro brachycephala*

FIG. 5. Arrangement of tubercles on dorsum and proximal tail. (A) *Echinosauro panamensis* (ZFMK 49107); (B) *Echinosauro palmeri* (BMNH 1923.10.12.14); (C) *Echinosauro horrida* (ZFMK 43768); (D) *Echinosauro brachycephala* (ZFMK 46370); (E) *Teuchocercus keyi* (MHNG 2284.59); (F) *Echinosauro orcesi* (NMW F 3377). Drawings by Mathias Günther.

- 1b. Three or 5–6 ventral scales per caudal segment; postmental scale not reduced, reaching beyond one-third of first infralabial . . . 2
- 2a. Internasal single 3
- 2b. Internasal divided 4
- 3a. Three ventral scales per caudal segment; continuous paravertebral rows of enlarged scales present; 8–9 femoral pores (one side) in males, one in females *Echinosauro horrida*
- 3b. 5–6 ventral scales per caudal segment; continuous paravertebral rows of enlarged scales absent; 14–15 femoral pores (one side) in males, 5–6 in females *Echinosauro orcesi*
- 4a. Some or all of tympanum covered by granular scales; tail of adults bearing whorls of greatly enlarged conical spines; postmental scale small, not reaching beyond two-thirds of first infralabial *Teuchocercus keyi*
- 4b. Some or all of tympanum not covered by granular scales; tail of adults not bearing whorls of greatly enlarged conical spines; postmental scale large, reaching beyond two-thirds of first infralabial 5
- 5a. Frontal single *Echinosauro palmeri*
- 5b. Frontal transversely divided *Echinosauro panamensis*

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APPENDIX 1

Comparative material examined (* = specimens used in the discriminant function analysis).

Echinosauro orcesi.—**Ecuador**—Carchi: San Marco, 670 m: NMW 32000:1*; San Marco, 700 m: NMW 32000:2*.

Echinosauro horrida.—**Ecuador**—“Ecuador”: ZFMK 7269*–7271*, 7272; “Pacific versant of Ecuador”: ZFMK 43757*, 43758, 43759–63 (all*), 43764, 43765–72 (all*), 43773–74, 43775*–76*, 43777–81; Esmeraldas: near Mataje, 350 m: NMW 32001:1; Imbabura: Lita: SMF 11752; Paramba: AMNH 13402–03, MCZ 11172; Manabí: El Carmen, W of Santo Domingo de los Colorados: ZFMK 42760, 46369*; Pichincha: Centro Científico Río Palenque, 200 m, 47 km S Santo Domingo de los Colorados: AMNH 119827*–28*, MCZ 147175, 149670*–71*, 156140, 156148, 156149*, 156150–51, 156152*, 156153, 156154*, 156155–56; 4–5 km ESE El Esfuerzo, approximately 320 m in boulder strewn stream valleys: MCZ 171866*; Río Baba, 5–10 km SSW Santo Domingo de los Colorados: AMNH 110612.

Echinosauro palmeri.—**Colombia**—Cauca: Quebrada Guaguí, 0.5 km above Río Patia (upper Saija drainage), 100–200 m: AMNH 109695–97 (all*); Chocó: Noananoá, Río San Juan, 30 m: BMNH 1923.10.12.14; Quebrada Taparal, lower Río San Juan (about 7 km airline NE Palestina); AMNH 123710*–11*; Valle: near Cisneros on Buenaventura-Dagua Road: AMNH 108994. **Panama**—Darién: no specific data: AMNH 49186*–87*, 49190, 49195*; Chalichiman's Creek: AMNH 49200*.

Echinosauro panamensis.—**Panama**—Coclé: El Valle de Antón, stream on N side, 610 m: AMNH 71707*–08; El Copé: ZFMK 45779*, 49107*, 50084*–85*, 50462*, 50464, 52200*, 54631*, 64837*; Panamá: 2.5 km N Agua Clara rain guage on Santa Rita Lumber Rd (E of Colón): MCZ 133722; Cerro Campana: MCZ 127763*.

Teuchocercus keyi.—**Ecuador**—Carchi: Río Sabalera, 620–630 m: NMW 31988*, 32001:6–8; Río Sabalera, near Ojala, 630 m: NMW 32001:2–4; Ojala, 400 m: NMW 32001:5; Esmeraldas: 1 km W El Placer: USNM 196094*; Río Mira, 620 m, NMW 32001:9–11; Pichincha: 4 km E Río Baba bridge, 24 km S Santo Domingo de los Colorados: UIMNH 80452; Puerto Quito: MHNG 2284.059*.